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AN HISTORICAL STUDY OF THE MIGRATIONS OF *CELERIO LINEATA LINEATA* FAB. AND *CELERIO LINEATA LIVORNICA* ESP. (LEPIDOPTERA)

By Mrs. K. J. Grant.

(*Rothamsted Experimental Station.*)

[Read 5th May, 1937.]

Since early in 1931 the South-Eastern Union of Scientific Societies has been encouraging the collection of records dealing with the migration of insects in the British Isles, and a special Insect Immigration Committee has been set up to organise the efforts of amateurs and others who are interested in this branch of entomology. As a result of the Committee's activity, a great deal of useful information is collected yearly and sent to Rothamsted Experimental Station, where it is available for examination and analysis. Some very interesting facts and theories are already beginning to emerge from this steadily accumulating mass of data, but it suffers somewhat from the drawback of dealing only with current events, and many years must pass before one can expect by its means to throw much light on underlying problems such as periodicity, correlation with climatic factors, or the relationship between migrations in the British Isles and those in other parts of the world.

Another store of information is, however, available in all those periodicals and journals which have for a century or more been in the habit of devoting part of their space to records of the observations of collectors and naturalists in all parts of the world. From these it seemed that it might be worth while to make an investigation into the past history of one or two individual species for comparison with the more recent records of the Insect Immigration Committee.

In 1931 *C. lineata* var. *livornica* became unusually common in western Europe, and was reported to the Insect Immigration Committee in greater numbers than it had ever before been recorded in Great Britain. This led to its selection for the present investigation, and it has proved to be a very suitable subject in many ways. Not only is it rare enough in this country to have received a good deal of attention from collectors, but in other parts of the world its larvae are occasionally a pest of vines and other cultivated plants, and its years of unusual abundance have therefore been recorded from time to time in the economic literature. In addition, the information available is sufficiently abundant to provide an adequate basis for investigation, without being so copious as to prove unmanageable. In fact the species might almost have been designed to suit the purposes of the work in hand.

Distribution.

The moth generally known in this country as *Celerio* (*Deilephila*, *Phryxus*) *livornica* Esp. is the old-world sub-species of the Sphingid *Celerio lineata* Fab., the nominal form being confined to America. A third sub-species, *Celerio l. livornicoides* Lucas, is found in Australia, but so little is known about it, and it has so seldom been recorded in any abundance, that I do not feel justified in dealing with it here.

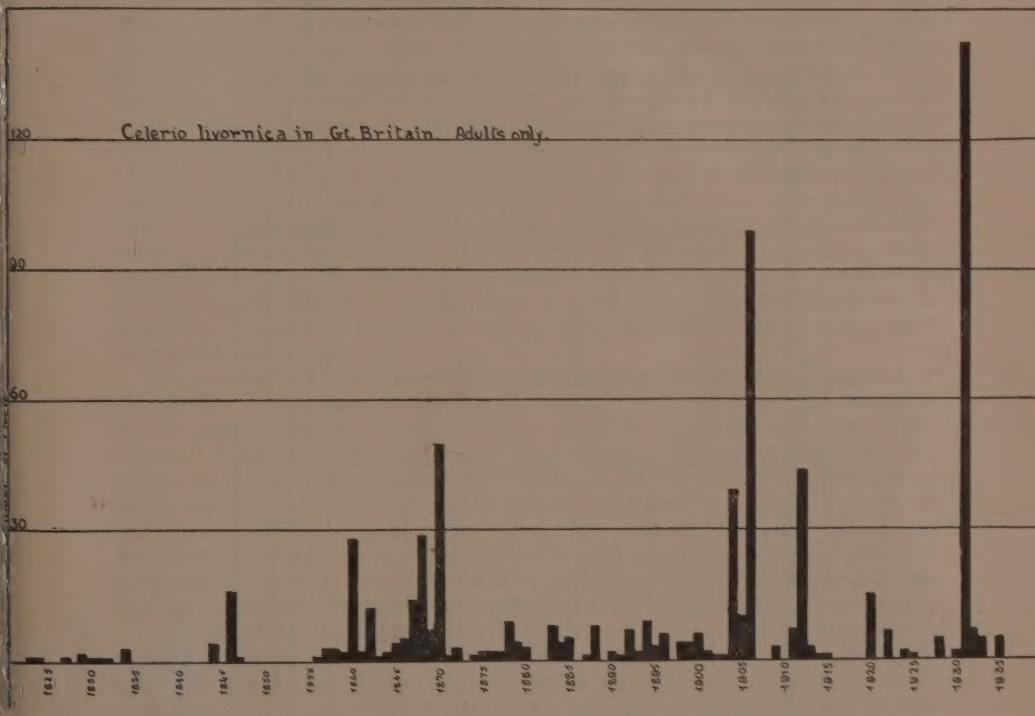
C. lineata and *C. l. livornica* are very similar both in appearance and habit, but they appear to form perfectly distinct geographical races, and there is sufficient difference in their markings and gross morphological detail to prevent their confusion when seen side by side. *C. lineata* has been seen from New Jersey to Ecuador, and *C. l. livornica* from China to western Europe and southward to the Orange Free State, yet in neither case is the permanent habitat (if any) known with any degree of certainty. In some of the warm-temperate parts of the northern hemisphere they have been seen frequently enough to give the casual observer the impression that they are indigenous, but a closer examination of the literature suggests that they are usually migrants from elsewhere. *C. l. livornica*, for example, is fairly frequently seen in the African littoral of the Mediterranean, and occasionally appears there in great abundance as a pest. Many years may pass, however, without a single record coming from this area, and when the larvae ravage the vineyards in years of abundance, the cultivators seem to regard them as an unusual pest. In various parts of Europe the moths have been abundant in about one-third of the past sixty years, and small numbers have occurred more often, yet the species has nowhere permanently established itself, and it may be absent for years on end. The same seems to be true of the American sub-species, which is common in some seasons in many parts of the United States, but can hardly be said with certainty to be indigenous in any particular district.

Outbreaks of both sub-species are most frequent and abundant in the neighbourhood of deserts and semi-desert areas; for example, California, Utah, Arizona and other States surrounding the Great American Desert; Morocco, Algiers and Tunis, near the Sahara; and Anatolia, the Caucasus, southern Russia, and Persia, near the deserts and arid steppes of Asia Minor. The only reference I have been able to find to an outbreak in South America took place in 1925 in the Santa Elena Peninsula, a desert district in Ecuador, during the first rains that had fallen for several years. One may perhaps venture to suggest that one is dealing with a desert species which, in response to unusual conditions of climate or to some similar stimulus, sometimes outbreeds the resources of its normal habitat, and is forced to migrate elsewhere. American entomologists would probably agree with this view, since they often find *lineata* especially common on the outskirts of deserts in its years of abnormal abundance. The habits of the larvae are quite compatible with this supposition. They occur on all sorts of low-growing plants and weeds, and not only the species but even individuals are extremely polyphagous. On several occasions it has been observed that when a large number of larvae have completely destroyed the food plants on which they were hatched, they will migrate gregariously, examining everything in their path, until they have found a sufficient growth of something suited to their taste; this may be a species belonging to a different family or even to a different natural order from that on which they started life. Behaviour such as this would have a definite survival value for a species dependent for its food supply upon the sparse flora of desert areas. An interesting account of such a mass migration of larvae is given by J. Brunetau (1932, *Rev. Zool. agric.* **31** : 9), and may be translated as follows: "In the commune of Bors de Baignes quantities of larvae devastated about a hectare of buckwheat, leaving only the stalks and reducing the plantation to skeletons. Lacking food the ravagers descended to the ground in millions, and moved off browsing on *Rumex* by the way, until they reached a plantation of cabbages. Some of them climbed on to these plants, but they were soon abandoned, and at last they reached a vineyard, which they began to misuse. Parts recently sulphated

were respected, but the young growth, the leaves where the Bordeaux mixture was less apparent and even the twigs were damaged."

Celerio livornica in Britain.

Whatever may be the stimulus which releases the migratory impulse, it is very strong when once aroused. If Africa be the source of the majority of specimens of *livornica* caught in Great Britain in spring, a fact which there is little reason to doubt, journeys of a thousand miles or more must frequently have



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been flown. Great Britain has been reached in at least seventy-two of the 113 years since the species was first found here (fig. 1), and although in most of these years only one or two individuals have been seen, there have been occasions when comparatively large numbers must have been present. In 1870, for example, at least seventy moths and larvae were recorded; in 1906 the numbers reached one hundred and in 1931 over one hundred and fifty individuals were seen, among them both adults and larvae. It should not be thought that these rising figures represent an actual increase in the numbers reaching Britain; they are much more likely to indicate the larger number of persons taking an interest in the matter. But it is reasonable to suppose that fig. 1 does give a more or less true picture of the relative abundance and scarcity in various years. It is unlikely, for example, that the number of observers decreased materially

Celerio Livornica in Britain - (Larvae in Brackets)

Year	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	No. date	Year's Total.
1823						1								1
24						1								1
27													1	1
29													2	2
1830													1	1
31							1							1
32							1							1
34							3+(2)							3+(2)
1844						4								4
46				9	1	2							4	16
47													1	1
1856													1	1
57													3	3
58				1	1	1								3
59													2	2
1860					18	1	6						3	28
61	1	1												2
62			1	3	6	1							1	12
63						1								1
64													2	2
65									2	1			1	4
66					2								3+(1)	5+(1)
67					8		1						5	14
68				1			2	20	2				4	29
69					3			1					3	7
1870				1	11	12	1+(10)	11	7	1			6+(10)	50+(20)
71													1	1
72						1			1				1	3
74						1								1
75					1								1	2
76													2	2
77						1		1						2
78						5	1	3						9
79						4								4
1880									2				1	3
83						2	4						2	8
84						1	2		1					4
85													5	5
87		1												1
88						6							2	8
1890									2					2
91									1					1
92					1	5							1	7
93					2									2
94						8	1							9
95						1	1		1					3
96					3		1	1					1	6
98					1	1				1			1	4
99					3			1						4
1900					2	1	2						1	6
1						1		1						2
2							(1)						1	1+(1)
3			1											1
4					31	3	(1)	1	4					39+(1)
5				7				1					2	10
6					19	69	1+(1)	2	6				2	99+(1)
9				1			1			1				3
1911						1	1	2	2				1	7
12	1	1			41								2	44
13						2			1					3
					1									1
15					1									1
1920					14	(1)	1							15+(1)
22					5		(1)						1+(1)	6+(2)
24					1		1							2
25					1			(1)						1+(1)
28				1		1	1		2					5
1930								2						2
31					31	100	1+(16)	(12)	1				9	142+(28)
32						2	(5)						5	7+(5)
33							(6)	2	1		2			5+(6)
35				1	1			1					2	5
Adults	2	2	2	25	209	240	34	50	36	4	2	0	87	693
Larvae						1	43	13					12	69

from 1906 to 1907, yet the number of *livornica* recorded fell from one hundred to nil; again, from 1931 to 1934 the number of observers reporting the presence of migrants to the Insect Immigration Committee rose steadily, yet records of *livornica* fell from more than 150 in 1931 to 12 in 1932, 11 in 1933, and none in 1934.

Fig. 2 shows the seasonal distribution of all the individuals shown in fig. 1, with the addition of larvae, the numbers of which are given in brackets. In some cases, the date of capture, apart from the year, is not known; such insects are shown in the column before the year's total.

It will be seen that the species has been found in every month of the year except December; May and June being those in which it is most numerous. Larvae are more common than adults in July, and the subsequent increase in the number of adults in August and September may be taken as evidence of the emergence of a British-born generation. An interesting comparison may be made between *livornica* and those migrants which, like *Vanessa atalanta*, *Vanessa cardui*, *Plusia gamma*, etc., visit this country every year in fairly large numbers. In these cases the autumn emergences are almost invariably far more numerous than the spring arrivals, showing that our summer conditions are suitable, and that it is only inability to pass the winter here that prevents the species from gaining a permanent foothold. In *livornica*, on the other hand, the autumn generation is rarer than that of early summer; our conditions must be unfavourable to the species even at the best time of year, and even should they succeed in passing a winter or two, they must die out in time unless reinforced by fresh migrants from the south.

The number of moths found in Great Britain from November to March is over 1% of the total, a surprisingly large amount. If *V. atalanta* were found in similar proportions, for example, many hundreds would be seen here every winter. While most of those found in April may be early immigrants (the species is active in Mediterranean districts in March) the occurrence of even single specimens in January and February suggests that hibernation is not entirely impossible, even if it be infrequent. The experience of those who have reared the species in captivity shows that the pupal stage is short, the moths emerging three or four weeks after pupation. There is no account of the finding of the pupa in winter in this country, or, indeed, anywhere else in Europe.

The occurrence of these unusually early individuals does not necessarily either precede or follow years of abundance; indeed, in one case a February specimen was caught during a period when the species was almost absent from Europe. This moth was shown at a meeting of the South London Entomological Society in 1887, and there can be no question of its correct identification. The account of its capture given by Mr. J. A. Helps (1887, *Entomologist*, **20** : 157) is so interesting that it is worth quoting here in full.

> "On April 18th last an old servant, living with her father at Coles Cross, near Crewkerne, sent me a specimen of *Deilephila livornica*, which flew into their cottage (attracted by the light) in the beginning of February last. She states that they caught one last year, and that a neighbour took one the previous year, about the same date."

Apart from this one specimen (the other two mentioned in Mr. Helps' letter were not included in figs. 1 & 2, owing to lack of reliable identification) I have been able to trace no other record of *livornica* in 1887 in the whole of Europe, and only one in 1886, a single individual in Hesse, Germany.

The sex is recorded in eighty-five of the *C. l. livornica* found in Great Britain,

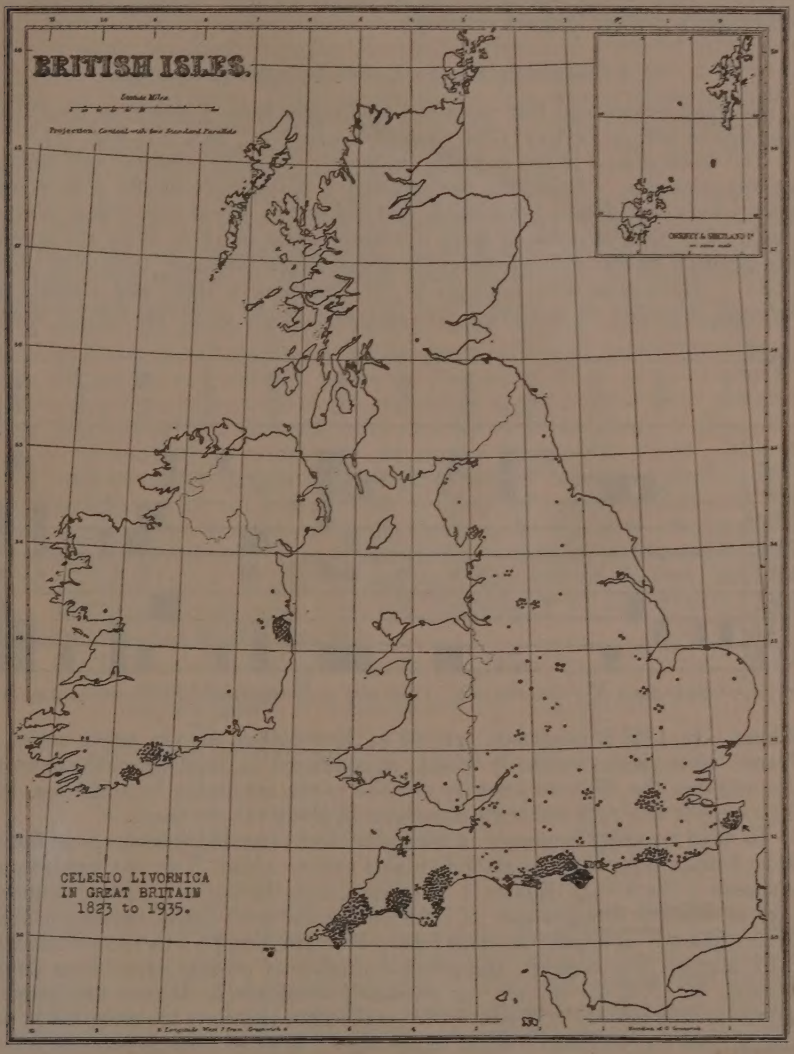
the proportions being fairly near to equality, *i.e.* forty males to forty-five females. Comparatively few of the continental specimens have been sexed, and in these the females outnumber the males by thirty-three to six. Part at least of the preponderance of females may be accounted for on the assumption that many individuals were only sexed at all as a result of their laying eggs, the sex in other cases being ignored. Nevertheless, there is some reason to suppose that the species is one in which the females normally outnumber the males. On one or two occasions, small numbers of imagines have been reared from eggs laid by captive females, and the sex of all the resulting moths has been recorded. In one such experiment, thirteen eggs gave rise to nine adults, eight of which were females, and in another an equal number of eggs gave rise to two males and four females. More information is needed on this point, and it is hoped that when next the species appears in quantity, observers will be careful to determine the sex in as many cases as possible.

The map in fig. 3 has been drawn to show the distribution of all *C. l. livornica* seen in Great Britain between 1823 and 1935, both adults and larvae, except for a few specimens whose locality I have been unable to trace. A separate map was originally drawn for the moths seen in late summer and autumn; it was thought that this might show a breeding area smaller than that reached by immigrants. This was not so, however; the two maps were essentially similar, and were eventually combined to form fig. 3, which now shows the location of all records, irrespective of season.

Naturally such a map is influenced by the distribution of human population. The large empty spaces shown in such areas as central Ireland and the mountains of Wales, where there are few people and fewer entomologists, probably received their quota of moths like other places, but the insects arrived unobserved and passed unseen. In estimating the local abundance of insects, however, there is one clue which does not depend on human population, and which may be used as a rough guide to relative numbers in different places. This is the number of insects seen by each individual observer. If this correction be applied to the present map, it is found that it only intensifies the tendencies that are already apparent. In the Midlands and North, the appearances are almost invariably solitary, and at intervals of many years. Along the south coast, the species occurs more frequently, and the same observer sometimes reports two or three individuals in a single year. But the greatest numbers are found in the extreme south-west and in Ireland. From Cornwall are records of as many as twenty-five specimens taken by a single collector in one year, while in Ireland, twenty-one *l. livornica* were seen at Timoleague, Co. Cork, in 1931, and thirty-two were reported from Shankhill, Co. Dublin, in the same year, by single observers in each case.

This tendency to greater abundance in the west is found in other migrants besides *l. livornica*, and gives rise to some interesting speculations. A glance at the map of Europe shows that if a migration leaves the western part of north Africa travelling northwards, after it passes Lat. 44° a part of it will have to cross the plains of France, and a part the Bay of Biscay. It is reasonable to suppose that the section flying over France will gradually thin out as it goes northwards, many individuals ceasing their migration and settling in France long before the Channel is reached. Those farther westward, however, will find themselves crossing the open sea, and will be unable to stop until they reach Cornwall, Ireland, or the shores of the Irish Channel. They will thus arrive with their numbers unimpaired, except by the loss of such individuals as have fallen into the sea and been drowned.

There is very little evidence of insects actually seen crossing the Bay of Biscay; one or two records do exist, however, and the arrival of butterflies in the Scilly Islands, where they are reported flying northwards in from the sea,



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suggests that it is not impossible for them to do so. It may be objected that the four hundred miles from Spain is an unlikely distance for insects to fly at a single stretch, and that most individuals attempting to do so must inevitably perish, but it seems likely that migrating insects may be able to refresh themselves by floating for a while on the surface of the water. Miss

Longfield told me that she has seen a hawkmoth alight on the surface of a pool in Ireland, and rise from it again, and the keepers of lightships have on several occasions reported similar behaviour on the part of migrating Pierids. If this ability to rest on the water is at all normal, it must be of great assistance to Lepidoptera making long sea crossings.

C. l. livornica in Europe and *C. l. lineata* in America.

Celerio livornica was first described by Petiver from a specimen caught as long ago as 1698 in Lisbon (1764, *Gazophylacium* **1** : 2, Tab. XL, Fig. 11).

The description is of the vaguest, but luckily the moth is figured well enough for identification. During the next century a few solitary adults of both subspecies were captured and described, and one or two larvae were found in vineyards. The first mention of large numbers occurs in 1818, when the species was plentiful in Switzerland especially round Berne (Meisner, 1818, *Nat. Anz.*, **1** : 44). The moths were common in the Caucasus in 1829, and a single individual, probably on migration, was seen at a height of 12,000 feet on Mount

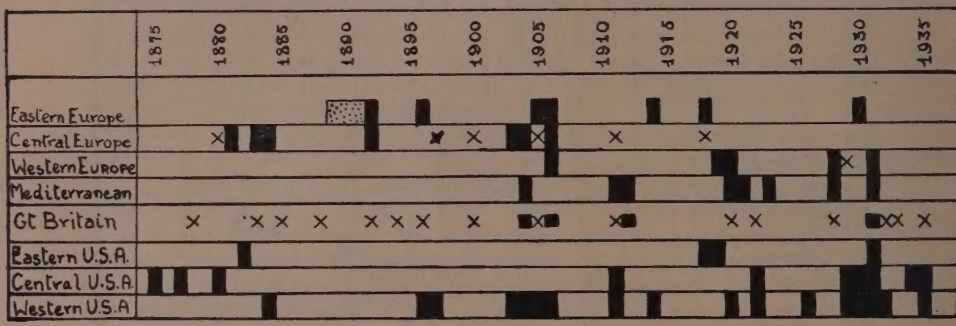


FIG. 4.—Comparison of outbreaks of *C. l. livornica* in Europe and *C. l. lineata* in America.

Elburz. In 1835 a migration arrived at Montpellier, on the south coast of France, after violent southerly winds; it is difficult to decide from the description whether the observer actually saw the moths coming in from the sea, but they were at any rate suddenly abundant all along the sea front.

In 1846 numbers appeared in Germany, and extended westwards as far as Great Britain, where twenty-six individuals were recorded. Twelve years later an outbreak in the Alburs (Elburz ?) Mountains, near the Caspian, had no counterpart in western Europe, and in 1864 the moths were again common in Asia Minor, but not unusually so elsewhere. Western Europe was next visited in 1870, and on this occasion the greater number of records came from Great Britain; in 1874, the species was unusually abundant in Algiers, and present (numbers unspecified) in Persia. Outbreaks after this date are recorded in fig. 4, and need not be listed further in the text. That of 1883 is perhaps worth special reference, since in this year the moths were extraordinarily abundant all over central Europe, but apparently nowhere else.

It seems extraordinary that no mention of the damage done by the larvae should be made in European literature until 1904, although *C. lineata* had been recognised for some time in America as an occasionally severe pest of vines. The damage done, however, is very sporadic and local, and it was not until well into the nineteenth century that entomologists began to take an interest in the

practical aspects of their science; even then they largely confined themselves to the more important pests. It is probable that outbreaks occurred from time to time in Europe, but no one took any notice of them except the unfortunate farmers whose crops were attacked. Once attention was attracted to it, *l. livornica* was found to infest a great number of wild and domesticated plants. In cultivation, the most important host is the vine, and when the larvae are present in large numbers they will strip the plants very quickly, devouring even shoots and young grapes. Other plants besides vines are sometimes attacked; among them are olives (Tunis, 1904); cotton (Spain, 1928); buckwheat (Caucasus 1930 and France 1931). In addition to these hosts, the American sub-species has also been reported from tobacco (Jamaica, 1922).

Fig. 4 has been prepared to show in the form of a graph all outbreaks that have been traced in Europe and North America since 1875, the year when the first American outbreak was recorded. Particulars of most of these American outbreaks were sent me by the United States Department of Agriculture, but some half dozen additional records were obtained from various journals. The black areas in the graph represent years in which definite outbreaks occurred; the shaded area in eastern Europe for the years 1889–1891 represents a period when the species was certainly present in Rumania, but its numbers were recorded in such vague terms that it is impossible to say whether there was anything comparable with the outbreaks recorded in other places or not. The crosses represent the occurrence of the species in numbers which, although small, were unusually high for the latitude concerned; they may possibly have been connected with outbreaks farther south which passed unnoticed. The most surprising fact brought out by this figure is the degree of correspondence between years of outbreak in America and those in Europe; of the sixty years that have passed since the first outbreak was reported from America, there has been correspondence in forty years and dissimilarity in only twenty. The following table will make this clear:

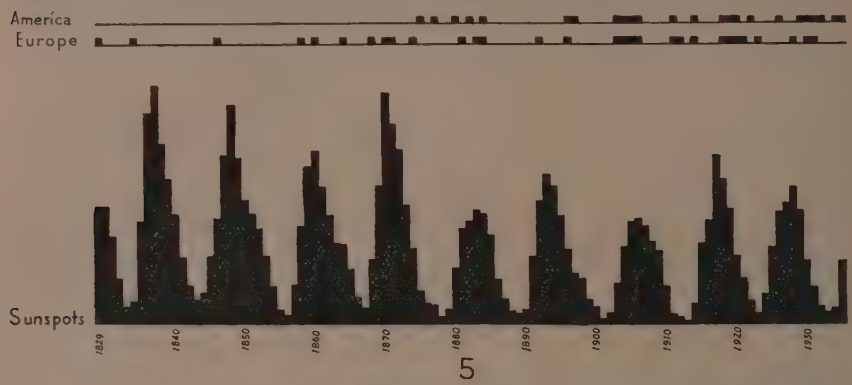
Outbreaks in both continents: 13	In America only: 10	In America: 23
In Europe only: 10	In neither: 27	Not in America: 37
In Europe: 23	Not in Europe: 37	Total: 60

Thus, of the twenty-three years when there were outbreaks in Europe, only ten years were without an outbreak in America; in the thirty-seven years when there were no outbreaks in Europe, they occurred only ten times in America. If the three doubtful years mentioned above, 1889, 1890, and 1891 be counted as years when no outbreak occurred, the correspondence becomes stronger, with forty-three years in which the continents resembled one another, and only seventeen in which they differed. It is most unlikely that figures such as these should be due to accident, the chances against it being about twenty-two to one if the three doubtful years in Rumania are counted as outbreaks, and greater than a hundred to one if they are not. It will be seen that the crosses representing small numbers in unlikely places tend to strengthen the correlation between Europe and America rather than to weaken it.

The implication of all this is clear. In seeking for an explanation of the

outbreaks of *l. livornica* and *l. lineata*, one must look for some large cause, wide enough in its effects to have influenced both continents simultaneously. One or two authors have, for example, put forward the suggestion that forest fires or the passing of locusts or grasshoppers may have caused the multiplication of the moths, by cutting back the larger trees and shrubs, and so encouraging the growth of the lower plants on which the larvae feed. But this will not satisfy the new requirements, since a forest fire in America will not benefit *l. livornica* in north Africa, neither can the incidence of African locusts have much effect on *l. lineata* of America. Incidentally, it has yet to be shown that either sub-species ever occurs in forests, or near enough to them to gain by their temporary destruction.

A possible explanation of the coincidence between outbreaks of sub-species in two continents would be that both were subject to a periodicity of the same length, and that the periodicities were in phase with one another. A glance at figs. 1 and 4 will show, however, that there is no regular periodicity.



5

An example of a somewhat irregular periodicity to which much has been attributed in recent years lies to hand in the sunspot cycle. Sunspot activity can be measured by counting the number of spots each year, and the figures of such counts are available for the whole period covered by the work on *l. livornica*. The number of spots varies from none (1810) to 137 (1837); more general minima being 3 to 5, and maxima 80 to 90. The maxima occur on an average every eleven years, after which there is a fairly gradual fall towards the minimum, followed by a more rapid rise to the next maximum.

There does seem to be some relationship between the outbreaks and sunspot cycle, as shown in fig. 5, which may be expressed in tabular form as follows :

		Total.	Minimum to Maximum.	Maximum.	Maximum to Minimum.	Minimum.
Years		107	32	11	54	10
Outbreaks	To be expected in absence of correlation . .	—	12·3	4·2	20·7	3·8
	Observed . .	41	14	6	20	1
	Difference .	—	+ 1·7	+ 1·8	− 0·7	− 2·8

There have been forty-one outbreaks in the past 107 years, and if there were no connection between outbreaks and sunspots, this proportion should be preserved throughout. The figures predictable on this basis are given in the second line of the table, and in the fourth line the difference is shown between these figures and the actual outbreaks recorded. The number of outbreaks would seem to rise from the minimum towards the maximum, and then to fall away again towards the next minimum, the difference between predicted and observed values being greatest at the year of minimum activity, where the figures are just significant. But the possibility of the apparent connection being due to chance is not precluded; it is worthy of note that some of the most recent and widespread outbreaks (1930–1932) have taken place during a period of rapidly falling activity.

Reference has been made earlier to the possibility of climate influencing the outbreaks of this moth, and rainfall immediately comes to mind as the factor most likely to be effective. While rain is usually supposed to be absent

	Nevada				Utah		Arizona		Colorado		New Mexico	Total Plus or Minus		Wet or Dry	Imeata outbreaks
	Battle Mt.	Toiopah	Fallon	Montello	Moab	Salt Lake City	Yuma	Phoenix	Colorado Springs	Las Cruces	Agricultural College	+	−		
1907	−	+	+	+	+	+	+	+	−	+	+	8	3	W	
8	+	+	−	−	−	+	−	+	−	+	−	5	6	D	
9	+	−	−	+	+	+	+	+	+	+	−	8	3	W	
1910	+	+	+	+	−	−	+	−	+	+	−	7	4	W	
11	+	+	−	−	+	−	+	−	−	−	−	4	7	D	X
12	+	−	−	−	+	−	−	+	−	+	−	4	7	D	
13	−	+	+	+	−	+	−	−	−	−	+	5	6	D	
14	+	+	+	+	+	+	−	−	+	+	+	9	2	W	X
15	+	+	+	+	+	−	+	+	+	+	+	10	1	W	
16	−	+	+	+	+	−	−	+	+	+	−	7	4	W	
17	−	+	−	+	+	+	−	+	−	+	−	6	5	W	
18	−	−	−	−	−	−	−	−	−	−	−		11	D	X
19	−	+	+	−	+	−	−	+	−	+	+	6	5	W	X
1920	−	−	−	−	−	+	+	+	−	+	−	4	7	D	X
1	−	+	+	+	−	+	−	−	+	−	−	5	6	D	
2	+	+	+	+	+	+	−	−	+	+	−	9	2	W	X
3	−	−	+	+	−	+	−	−	−	−	−	3	8	D	
4	+	−	−	−	−	−	+	−	+	+	+	6	5	W	
5	−	−	+	−	−	−	−	−	−	−	−	1	10	D	
6	+	+	+	+	+	+	+	+	−	+	+	10	1	W	X

FIG. 6.

from deserts, it is not entirely unknown, especially on their outskirts, and when it does fall its effects are proportionately great. Unfortunately, very few figures seem to be available for the Old World deserts; it would seem that either there are no weather stations in the Sahara, or else that a rain gauge is not considered a proper part of their equipment. By courtesy of the London Meteorological Office, I have been able to obtain a few figures; most of them come from Egypt, but one or two series are from stations near to the more westerly part of the Sahara, and one is from Tiflis, in Asia Minor; most of the series are comparatively short and much broken. There does not seem to be any correlation between them and the outbreaks of *l. livornica*, but the figures are far too scanty for it to be said with certainty that no correlation exists.

From America, the United States Department of Agriculture Weather Bureau have sent me copies of their climatic summaries for the relevant States. Many of these summaries go back before 1875, the year of the first recorded *l. lineata* outbreak, and from them it has been possible to compile a table showing the departures from the annual mean rainfall in eleven scattered desert States. A portion of this table is illustrated in fig. 6. Since outbreaks tend to occur about June, the year's rainfall has been calculated from June to May, instead of from January to December, the more usual method. Where the stations showing a deficiency in any year outnumber those showing an excess,

it is counted a dry year; where the reverse occurs, it is counted wet. This gives a rough criterion by means of which it is possible to divide the period into years of relatively high and relatively low rainfall, as a basis for comparison with years when outbreaks of *lineata* occurred. The direct comparison of years of outbreak with the rainfall of the previous twelve months does not give a very promising result. There is a slight tendency for outbreaks to follow wet years, but the figures are not significant, and no conclusions can be drawn from them. If, however, the weather for two years preceding the outbreaks be taken into consideration the very interesting result is found that there is a distinct tendency for outbreaks to occur when a wet year has followed a dry year. These results may be summarised as follows :

		Total.	Dry years following dry years.	Dry years following wet years.	Wet years following wet years.	Wet years following dry years.
Years		60	22	13	11	14
Outbreaks	To be expected in absence of correlation .	—	8·4	5·0	4·2	5·4
	Observed . .	23	8	3	2	10
	Difference .	—	− 0·4	−2·0	− 2·2	+ 4·6

Here, the observed values are below those predicted in every column except the last, where wet years following dry years are shown. The figures are significant, and the chances against them having occurred by accident in this particular proportion are about forty-five to one. The interpretation of these results is by no means easy; indeed, it is difficult to make even an intelligent guess to account for the connection between this particular sequence of weather conditions and the subsequent migrations. One might imagine that the dry year forced the insects out to the edges of the desert area, and that if subsequent wet weather should stimulate breeding and produce over-population, the moths would migrate outwards to cultivated lands as well as inwards towards the desert again. But this is to indulge in pure speculation; the interesting point is that these figures do strengthen the suggestion that *C. lineata*, at least, is a species of desert or semi-desert origin. It is a great pity that the paucity of weather records do not permit us to check it by comparison with the African sub-species.

Acknowledgments.

My thanks are due to a number of people who have helped me with information about the occurrence of *Celerio l. lineata* and *C. lineata livornica*, and on other points which have arisen in the course of the work; to Dr. A. S. Hayt, of the United States Department of Agriculture, for information about the years of abundance of *C. l. lineata* in America; to the many observers of the Insect Immigration Committee, and to all those who have sent me particulars of *C. l. livornica* in private collections in this country. I am also indebted to the Secretary of the Royal Observatory, Greenwich, for data on sunspots, and to the Directors of the United States Department of Agriculture Weather Bureau and the London Meteorological Office for records of rainfall.

In particular my gratitude is due to Mr. W. G. Cochran, of the Rothamsted Statistical Department, for the patience with which he has helped me with the statistical parts of this paper.

References.

During the course of the work, about two thousand volumes have been consulted, and nearly a thousand abstracts have been made. To give a complete list of sources would involve many pages of print, and would probably be of very little practical value. A full index of references is preserved at the Rothamsted Experimental Station, where they may be consulted by anyone interested in the subject.

The chief publications studied were :

The Entomologist.
The Entomologist's Monthly Magazine.
Annales and Bulletin de la Société Entomologique de France.
Annals and Magazine of Natural History.
The Zoologist.
The Review of Applied Entomology.
Horae Societatis Entomologicae Rossicae.
Boletin de la Sociedàd Entomològica de España.
Stettiner Entomologische Zeitung.

When an adequate index was present, such publications were taken volume by volume from their commencement. Many, however, had only lists of titles, and in these the method used was to pick a promising title, read the article concerned, and follow up any reference that might be given. A good deal of information was probably lost in this way, but the only alternative was page-to-page search, an impossibly lengthy task. Innumerable local lists of Lepidoptera for all parts of Europe were consulted, and some references were found in standard works, such as Tutt's *British Lepidoptera*, etc. Wherever possible such references were traced to their original sources, but this could not always be done, especially in the case of some of the earlier Russian writers. Some of the sources seem to have been privately circulated local lists in manuscript, and others I have been unable to trace at all.

Summary.

The distribution and outbreaks of the sub-species *Celerio lineata lineata* Fab. in America, and *Celerio lineata livornica* Esp. in the Old World as far as they are known are described. It is suggested that both sub-species originate in semi-desert areas, and this idea is supported in the case of the American sub-species by showing that a correlation exists between outbreaks of the moths and a certain sequence of desert rainfall. No correlation is found between European outbreaks and the rainfall of those North African meteorological stations for which records are available, but this may be due to the paucity of suitable figures.

A full account is given of the occurrence of *C. l. livornica* in Great Britain, and the main European outbreaks are listed. A correlation is given to show that both years of unusual abundance and of absence tend to occur simultaneously in Europe and America, and that the cause of outbreaks must therefore be sought in some factor common to the two continents.

There seems to be some correlation between outbreaks and the sunspot cycle, but the figures are barely significant. The outbreaks tend to occur away from the sunspot minima.

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